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Natural resources and climate change: A study of the potential impact on Manila clam in the Venice lagoon

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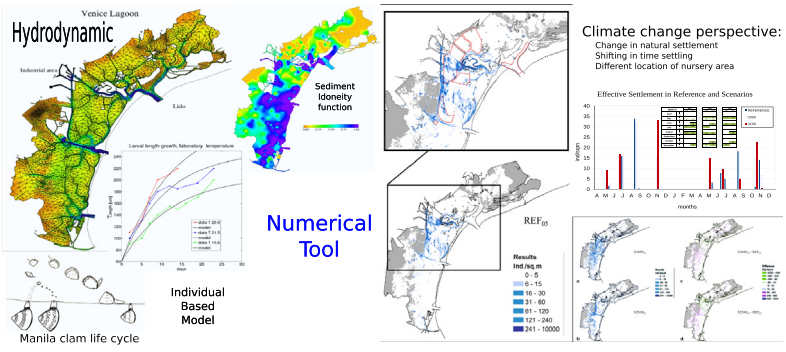
HIGHLIGHTS

- Knowledge of nursery and natural settlement is crucial for shellfish farm management.
- Combining hydro-bio-lithosphere for predicting Manila clams response to climate change.
- Numerical modeling can reproduce larvae settlement dynamics and nursery vulnerability.
- The model shows crucial features influencing larval settlings due to climate change.
- Presented tool can be used to develop a clever sustainable adaptive management.

GRAPHICAL ABSTRACT



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ABSTRACT

A crucial aspect in climate change is to understand how an ecosystem will adapt under different environmental conditions and how it will influence the ecological resources and the connected human activities. In this study, a numerical model reproduces the growth dynamics, dispersion and settlement of clam's larvae in the Venice lagoon. On the basis of the last IPCC scenarios for the years 2050 and 2100, the model simulates the changes in larval settlement, showing how the geographical distribution and, consequently, the nursery area changes over time.

Our results indicate that climate change will modify, not only the timing of the settlements (from spring–summer to winter autumn) and the spatial distribution of nursery areas (from central to southern lagoon), but also the absolute quantity of settled larvae in the lagoon. This can strongly affect aquaculture in terms of availability of seed and farming practice. Given that these changes are due to the variations in temperature and circulation, similar processes are likely to happen in other transitional environments all over the world affecting the global aquaculture resources. In this regard, the tool we developed could support local policy-makers in the knowledge-based planning and sustainable management of clam aquaculture in vulnerable environments.

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1. Introduction

Aquaculture is one of the fastest growing producing sectors in the world and experts have estimated it will supply 65% of all human seafood consumption in 2030 (Word Bank, 2013). Molluscan shellfish

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in 2012 accounted for 23% of total (inland and marine) aquaculture production and 60% of the world marine aquaculture production. The market is composed of 4 main groups of bivalva: clams, oysters, mussels and scallops represent the 80.7% of the total production. Italy is in the top 10 countries for mollusc aquaculture, representing the 0.7% of the world production (FAO, 2014). Italy is also the leader in Europe for this activity with the north-east Adriatic sea as the most productive area (Scientific, Technical and Economic Committee for Fisheries, 2014; Scarcella and Cabanelas, 2016), due to the presence of several shallow coastal lagoons.

Several authors (Boscolo Brusá et al., 2013; Gaspar et al., 2012) underline that some challenges to the full development of clam aquaculture still remain: 1) the availability of spat and 2) the management of nursery areas. The clam aquaculture is based on the seeding of spat and juveniles in the farm area. The production of seed is done artificially in specific plants, but they can offer only a limited number of seeds. Another way is to collect spat and juveniles from nursery areas, where they naturally are settled with high density. This "wild" seed is abundant, more economic and more resistant in the environment. Consequently it is very important to locate nursery areas and understand which factors contribute to create these natural settlement areas. The mixing practice of wild and laboratory seed is common in bivalve aquaculture (FAO, 2004), therefore, the sector relies also on natural settlements at the early life stage and recruitment. Thinking from a resource management and climate change perspective, a number of questions arise about how the clam culture will change and which effective management tools can help us to mitigate the impacts.

The Venice lagoon is a relevant example of the "wild-natural" seed mixing practices. The lagoon is one of the largest transitional systems of the Mediterranean where, for centuries human intervention has shaped the environment, exploiting its resources and where the management issue is a daily challenge. We developed a numerical tool to study how the clam culture will change in the future in the lagoon, as a relevant case study in terms of clam production value, data availability and need of integrated management.

Manila clam has a juvenile plankton spat stage and a benthic adult stage, with a time elapse between the two different life stages of about 20–30 days (Helm and Pellizzato, 1990; Paesanti and Pellizzato, 2000). During the planktonic stage the larvae are passively transported by the currents, therefore the adult organisms may grow in an area far from where they have been generated. The transition of the larvae from planktonic to benthic habitats exposes them to different environmental conditions and the early settled post-larvae presents a high level of mortality (Helm et al., 2004). The benthic stage, which includes settlement and post-settlement, plays a key role for the success of the overall recruitment process (Roegner and Mann, 1995).

An increasing number of biophysical models to predict the larval dispersal and settlement of marine benthic species is going to be applied in lagoons and estuaries because they provide important nursery grounds and adult habitat for exploited benthic commercial invertebrate. Starting from (Chícharo and Chícharo, 2001; Chićharo et al., 2001) modeling the growth of *Ruditapes decussatus* on the basis of temperature and water advection, other studies are moving toward high resolution hydrodynamic models coupled with complex larval dispersal models to predict the movement of particles taking into account the physical transport and larval behavior (Herbert et al., 2012). Settlement modules including also habitat suitability approaches are going to be applied to better understand recruitment success and post-settlement mortality (Hinrichsen et al., 2009; Bidegain et al., 2013).

In this study we developed an individual-based model of the *Ruditapes philippinarum* larval phase, adopting the lagrangian ensemble methods coupled with a spatially explicit hydrodynamic model. The larval development and settlement processes under different environmental conditions are represented by a metabolic module. The larval dispersion is simulated associating the metabolic module to a particle tracking module coupled to a finite element hydrodynamic model. The obtained tools simulate the population history representing the development of individuals, allowing us to assess the evolution and availability of the natural settled clam spat resource. We calibrated the tool in the lagoon of Venice simulating the settlement of early stages under realistic reference condition. Successively, we modified the environmental variables according to the climate change projection proposed by Ferrarin et al. (2014) to study how climate changes will influence reproduction, growth, dispersion and settlement, and how it will affect the suitability of different lagoon areas.

2. Study site

The Venice lagoon is the most extended lagoon of the Mediterranean Sea, connected to the Adriatic Sea through three inlets which guarantee the water exchange: Chioggia (500 m wide, 8 m depth) and Malamocco (500 m wide, 14 m depth) and Lido (1000 m wide, 14 m depth) from South to North. The lagoon average depth has been estimated around 1.2 m and 75% of the total surface area has a depth of less than 2 m (Molinaroli et al., 2007). The sediment is mainly composed by clayey silt with a mud fraction around 80% of dry weight, with the proportion of mud fraction decreasing from the North to the South (Molinaroli et al., 2009).

Tide and wind are the main factors regulating water level, circulation and sea exchange (Umgiesser et al., 2004; Pirazzoli, 1991). The discharge of several rivers contributes freshwater giving rise to the brackish profile of the lagoon salinity (Ghezzo et al., 2011). The water temperature has a clear seasonal cycle varying between 3 °C to 24 °C, with maximum values greater than 35 °C and local minimum values less than 0 °C (Tagliapietra et al., 2011).

The Venice lagoon was characterized by an abundant and diversified phytoplankton community (Bernardi Aubry et al., 2004). The algal blooms generally start from the inner part of the lagoon and are fast extended to the whole lagoon. The trophic characteristic of the lagoon has changed reducing in time (Facca et al., 2014) and also the phytoplankton community followed this trend. Breber (2002) observed that larval stages take their diatom diet from the plankton, so checking the phytoplankton availability we see that it has been estimated to never be lower than 2 μg/l, meaning that, at least in the studied years, no limitation for the larval growth (Bernardi Aubry et al., 2013; Paesanti and Pellizzato, 2000) can be assumed.

The Manila clam (*Venerupis (Ruditapes) philippinarum*) was introduced in the Venice lagoon in 1983 by a regional governmental agency for experimental purposes (Pellizzato, 1990a), and subsequently it spread in the other coastal lagoons of the northern-east Adriatic Sea (Goro, Scardovari, Marano-Grado) demonstrating a great capability to colonize temperate shallow lagoons (Pellizzato, 1990b). Within a few years *V. philippinarum* it became the most important commercialized species in Italy, with 95% of the overall production coming from the Northern Adriatic area. In particular, the Venice lagoon production reached a peak of over 64,000 t y^{-1} equivalent to the 60% of the total Italian yearly production at the end of 90s (Pellizzato and Da Ros, 2005; Zentilin et al., 2008). The production has since followed an irregular trend, showing a drastic decline in the year 2000 and again an increase in the following years (Pellizzato et al., 2011; Ponti et al., 2017). Actually the trend of production is variable year-by-year.

The aquaculture activity from 1999 was limited because of its the pressure on the environment. The local authorities assigned to the fishermen specific parts of the lagoon, called "*concessioni*", to use as farming areas (G.R.A.L, 2006, 2009, 2011).

Besides them, the local authorities established some "Wild Seed Fishing" areas (shortly WSF, Fig. 1) designated for the fishery of wild seed, used to improve the strength of the cultivated one. These areas were chosen because of their high natural larvae settlement and recruitment, resulting from environmental interactions on the natural selection process.

A extensive literature is available on Manila clam and on the identification of the suitable areas for clams fishery and their potential production (see Melaku Canu et al., 2011; Melaku Canu et al., 2010; Solidoro et al., 2003; Pastres et al., 2001; Solidoro et al., 2000). However, the dynamics of clam larvae dispersion, settlement and recruitment in the Venice lagoon have not been sufficiently studied, even if the fate of early stages plays a role in the abundance and distribution of the adults.

3. Material and methods

The work flow used to simulate the larvae settlement is reported in Fig. 2. The hydrodynamic model simulates, for the whole basin, the water circulation, temperature and salinity (step one), the particles tracking module calculates the trajectories of each released particle using the hydrodynamic information and finally the individual based module simulates the growth and settling of each particle based on the water temperature. The steps are iterated for the duration of the simulation using the maximum admissible timestep to assure hydrodynamic stability (150 s). At the end of the simulation the settled particles in each box of the regular grid are multiplied by the sediment idoneity (varying between 0 and 1) calculated on the basis of sediment grainsize. The workflow is replicated for the reference simulation (realistic condition) and for both scenarios simulations (climate change hypothesis). All the spatial elaborations of the model results are performed with Qgis software while the percent elaborations are calculated using dedicated fortran scripts.

3.1. Individual based model

A hydrodynamic model based on the finite element method SHYFEM (www.shyfem.org) and applied successfully in various case studies (Umgiesser et al., 2004; Ghezzo et al., 2010), has been used in its 2D version to simulate the circulation of the water masses and the spatial and temporal evolution of water temperature in the lagoon. The SHYFEM model simulates two different types of transport: eulerian and lagrangian (Cucco et al., 2009). In the eulerian transport the coordinates of the system remain fixed in space and the fluid characteristics, such as water level, current velocity, temperature and salinity, are computed in every fixed location. In the lagrangian transport the particles position is followed and different coordinates are assigned to different particle. The trajectory of each particle is described by the spatial variation of his position calculated using the current speed as well as the turbulent fluctuation, as explained in Ghezzo et al. (2015).

In the individual based model, each lagrangian particle represents a pool of larval organisms (lagrangian ensemble method) characterized by identical physiological state (homogeneous pool). The state S of each particle k is described as:

$$S_k^{new} = S_k^{old} + F(T) \quad (1)$$

where S_k is a vector of attributes, representing the larval organism state including length, weight, age and settlement stage (water column or bottom) of the particle. The term T represents the water temperature in the position of the particle, depending on time and space. The state vector of each larval stage is recalculated every timestep, to integrate the effect of the new environmental conditions on the organism development on the basis of the functional relationship F. It represents the metabolic module, and simulates growth, death and settling processes of the larval pool associated with each

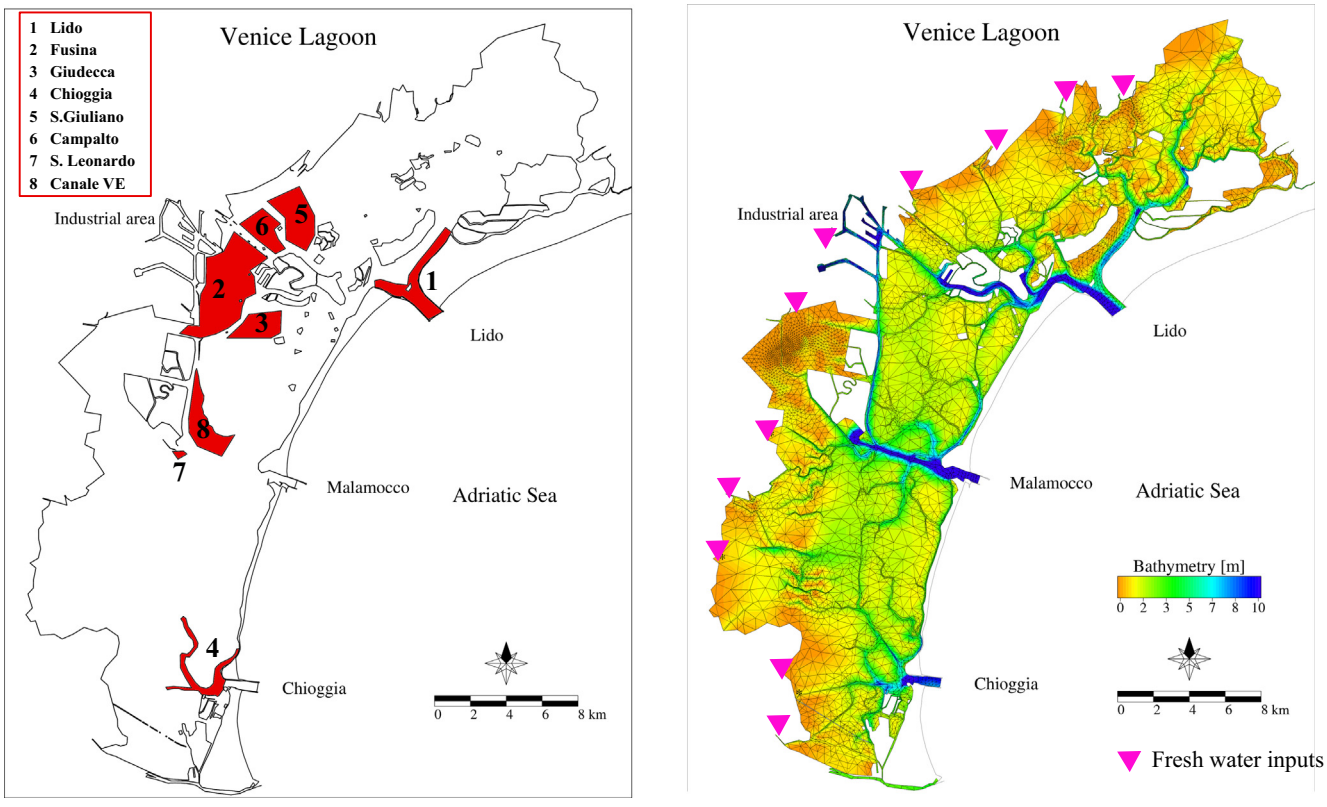

Fig. 1. Venice lagoon study site. Left panel: Wild Seed Fishing areas. Right panel: numerical grid, bathymetry and river outlets.

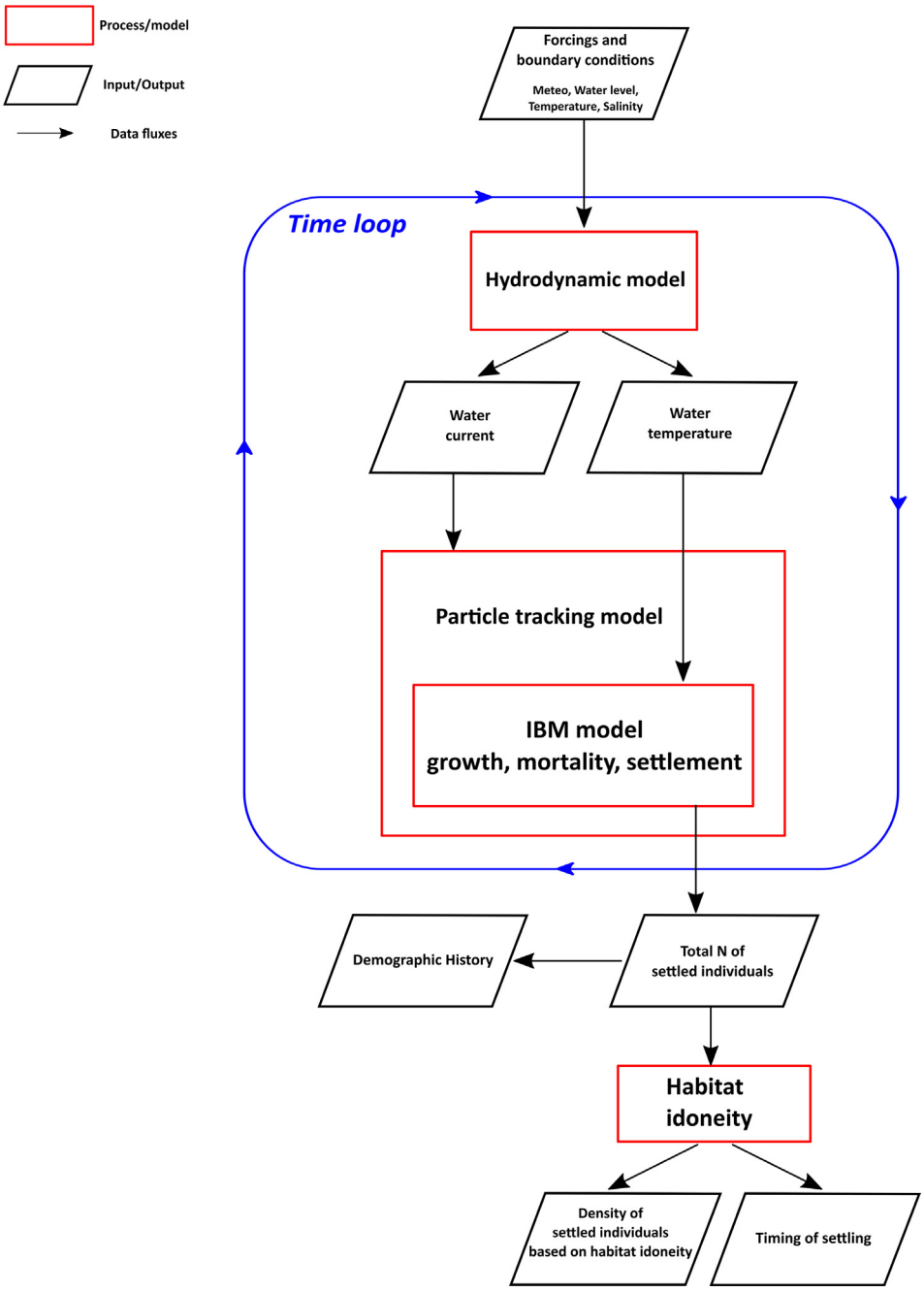

Fig. 2. Flow chart of the study.

lagrangian particle. Interactions between particles, vertical behavior of larvae and non neutral buoyancy of eggs are in a first approximation neglected, supposing that they are less relevant to define the larval dispersal in a shallow and vertically well mixed environment.

On the basis of the considerations reported in Section 2, we adopted, as a first approximation, the water temperature and the grain-size of sediments (Melia and Gatto, 2005) as main factors influencing the growth and the settlement of *R. philippinarum* larval stage in the Venice lagoon. The natural endogenous mortality of larval planktonic stages can be considered as dependent only on the sensibility to the water temperature, while for early new-settled organisms the mortality depends, to first approximation, on the sediment grain size composition. The larval mortality during the planktonic stage due to the exit from the lagoon and due to old age have been explicitly considered, whereas the mortality due to predation, fishery and density of settled organisms has been neglected.

Starting form the model proposed by Ursin (1967) for the fish growth:

$$dW/dt = A - C = beta * (1 - alfa)fhW(t)^m - kW(t)^n \quad (2)$$

the change of organism weight in time $W = W(t)$ is due to the balance between anabolic (A) and catabolic (C) terms. The anabolic term depends on the coefficient β, representing the fraction of consumed food really adsorbed, and α, the fraction of assumed food used for the

digestion process: this represents the total food available for growth. To complete the anabolic term the feeding level (coefficient f) and the food assimilation (coefficient h) are considered proportional to the body size W (in the form W^m in the equation). The catabolic term depends on a coefficient of catabolism without food (coefficient k) proportional to the body size (W^n in the equation). Empirical exponents m and n are related to the body size with the maximum possible assimilation, and to the body size with the oxygen consumption, respectively.

Assigning $m = 2/3$ and $n = 1$ the equation can be expressed in terms of length using the isometric relationship often used for fish and bivalva:

$$W = aL^3 \tag{3}$$

and thus the obtained equation is:

$$dL/dt = GL_{max} * f_a(T) - RL_{max} * f_c(T)L \tag{4}$$

where GL_{max} and RL_{max} are respectively the maximum rate of growth and the maximum rate of respiration expressed on the basis of the length. Functions $f_a(T)$ (anabolic) and $f_c(T)$ (catabolic) represent the dependence on the metabolic rates of temperature introduced in the equation following a multiplicative assumption. The reduced equation follows the von Bertalanffy growth function with the catabolic term $RL_{max} * f_c(T)$ depending linearly on the length, obtained also in this study by sensitivity analysis.

The temperature dependence functional form, adopted in anabolic and catabolic terms, is the one proposed by Lassiter and Kearns (1974) and Solidoro et al. (2000). In the case of low water temperature, it shows an exponential behavior; when water temperature approaches the optimal temperature value T_{opt}, it reaches its maximum value. For higher water temperature it has a decreasing trend, until the growth is reduced to zero when arriving at the maximum admissible temperature value T_{max}.

$$f(T) = \left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right)^{\beta(T_{max}-T_{opt})} e^{\beta(T-T_{opt})} \tag{5}$$

The particles mortality depends not only on the temperature but also on its dispersion outside the lagoon and on its Pelagic Larval Duration (PLD): the model considers as dead every particle exiting from the computational domain or older than 40 days (Shanks, 2009).

When the length of the larval pool associated to a particle is greater than an imposed threshold (220 μm), the particle instantaneously settles, stopping its growth and the influence of both hydrodynamic transport and water temperature. Only for settled particles the sediment grain-size composition contributes to the success of the larval settlement, therefore the number of settled particles in each element of the grid has been adjusted on the basis of a suitability function [0-1] defined as a linear function of the sand percentage in the element, following the ranges suggested by Provincia di Venezia (2009).

3.2. Numerical experiments design

The numerical tool has been applied in the Venice lagoon and every module has been calibrated by the comparison with field data. To estimate the effects of climate change on larval recruitment, reference and scenario simulations were performed and the difference in quantity and distribution of organisms were evaluated.

The reference simulation (REF) represents the period 2005–2006 under realistic forcing and initial conditions. In the text REF_{05} indicates the reference simulation in year 2005, REF_{06} indicates the reference simulation for 2006. The projections for years 2050 and 2100 were obtained changing forcing and boundary conditions, according to the seasonal anomalies reported in Ferrarin et al. (2014), in terms of water and air temperature, rain and water level, as reported in Table 1. Therefore the anomalies are added to the forcing of years 2005 and 2006 to create the scenarios S2050 and S2100 for year 2005 and 2006. The simulated scenarios for each specific year are indicated as $S2050_{05}$, $S2100_{05}$ and $S2050_{06}$, $S2100_{06}$. The changes to the river discharge, to the lagoon perimeter and to the salt marshes elevation were not considered.

In each simulation the lagrangian model with larval module was coupled in on-line mode to the hydrodynamic model, assuring the finest calculation of trajectories. The hydrodynamic simulation is two years long, from the 1st of January 2005 until the 31st of December 2006, with the lagrangian simulation starting from the 1st of April 2005 until the 31st of December 2006. This choice permitted us to reproduce the recruitment process in two different years, to evaluate its inter-annual variability and to investigate possible shifts in the period and settlement areas, limiting the number of particles and the computational time.

Following the data produced by the Intergovernmental Panel on Climate Change from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor et al., 2012) and the methodology described in Ferrarin et al. (2014), we defined the climate change scenarios considering the seasonal anomalies in water and air temperature, rain and water level, as reported in Table 1.

In the following specific set-up features for each numerical module are described.

3.2.1. Hydrodynamic setup

The SHYFEM setup is the same as used in Ghezzo et al. (2011) and Umgiesser et al. (2004), but the numerical grid was refined (Fig. 1, panel B) to improve the resolution and the morphological details in the shallower areas, so the bottom friction coefficients associated to each morphological areas (channels, salt-marshes, shallow areas and each inlets) are slightly modified to calibrate the water

Table 1
Seasonal anomalies adopted for climate changes in both scenarios. dz_{slr} sea level rise; dt_{sw} water temperature; ds_{sw} salinity; dt_{air} air temperature; *drain* precipitation; *dwind* wind speed. For each season the referred months are specified.

	2050				2100			
Season	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Variable	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON
dz_{slr}	0.30	0.30	0.30	0.30	0.63	0.63	0.63	0.63
dt_{sw}	1.97	2.01	2.13	2.06	3.38	3.50	3.89	3.67
ds_{sw}	0.34	0.34	0.39	0.40	0.62	0.61	0.70	0.72
dt_{air}	2.10	2.04	2.31	2.16	3.80	3.60	4.50	4.00
drain	0.17	−0.03	−0.13	0.04	0.31	−0.06	−0.23	0.08
dwind	−2.86	−3.46	0.00	−9.26	−5.14	−6.22	0.00	−16.67

levels. The lagrangian simulation starts 3 months after the hydrodynamic simulation, assuring a good spin up time for velocity and temperature.

The meteorological data adopted were collected with hourly frequency by the Italian National Research Council's Institute of Marine Sciences (ISMAR-CNR, Venice). The daily discharge of 12 rivers is included assuming the river water temperature equal to the air temperature. A preliminary analysis of the meteorological data (air temperature, relative humidity and rain plus wind direction and speed) indicated the reference year 2005 as an average climatological meteo-marine condition ("typical year"), whereas the reference year 2006 represents dry and hot year ("warm year").

3.2.2. Individual based model set-up

In the Individual Based Model, each released particle represents a pool of larval organisms at the first larval stage after fecundation, with initial length of 60 μm and settlement threshold of 220 μm.

The individual based model has been calibrated by a global optimization algorithm (Price, 1977) to estimate the best combination of seven main parameters with respect to the laboratory growth data under different temperature values (not shown). The obtained combination of parameters permits a good reproduction of the individual growth respecting the period employed to reach the threshold length.

The model assumes that the lagoon does not initially contain particles. The particles are released in areas corresponding to historical adults and juvenile populations, which were subject to a natural recruitment process ensuring high eggs emission (Pellizzato et al., 2011; Pellizzato and Da Ros, 2005).

In the model the emission process is performed simultaneously in all the designed areas, decoupled from environmental variables (temperature and salinity). We assumed the emission frequency on the basis of the gonadal maturation cycle and considering that the emission of an individual stimulates the others.

We performed a sensitivity analysis to define the emission frequency and the number of particle for each emission to reproduce the known distribution of benches of Manila in the lagoon (not shown). The result indicates the best emission frequency as two months starting from the first of April in the same initial areas (next generation) and inserting in the lagoon 500,000 new particles. This implies that, during the whole lagrangian run, there are 10 emissions and $5 * 10^6$ simulated particles. On the basis of this model implementation in year 2005 there are 5 generations, corresponding to the particles released in the model: released in April, June, August, October and December; in year 2006 there are 6: released in February, April, June, August, October and December. Emissions occur every 61 days, and each generation lives at most 45 days, so a peak of settlement can be produced only by two adjacent generations.

The last emission of particles is always at the beginning of October, so the analysis of the results in late November guarantees that they have had sufficient time to arrive to maturity and settle. For this reason we will always apply our analysis to the end of November.

The conversion factor ($F = 10^5$) to transform the number of particles to the number of organisms, has been estimated following Paesanti and Pellizzato (2000). The estimated density of organisms refers to square boxes with 100 m side length, made as regular grid covering the whole domain.

4. Results

The results are presented for the reference simulations and for the relative scenarios. Four typology of results were obtained: 1) Sediment suitability effect: the total number of settled particles in the whole basin both excluding and including the sediment idoneity (SI); 2) Spatial distribution: the spatial distribution of settled particles at the end of November of each year (considering SI); 3) Timing in settlement: the monthly settling timing (considering SI); 4) Demographic history: the history of population month by month (excluding SI). All the results are expressed in units of individuals to facilitate the comparison with field data. The results in the reference simulation are compared with available field data and the difference between 2006 and 2005 is used to estimate the inter-annual variability in settlement. The scenarios results are compared with the reference simulation calculating the difference with respect to the reference year 2005.

4.1. Reference simulation

4.1.1. Sediment suitability effect

The effective settled particles (it means taking into account SI) in the reference simulation in the whole lagoon are 50 ind/m^2 for each year (REF_{05} and REF_{06}). To estimate how strong is the SI selection in the lagoon, we compared how many particles reach the settlement threshold in each year, before and after considering the SI (Table 2). The number of settled particles in 2005 is lower than in 2006 (88 ind/m^2 vs 99 ind/m^2, first column), but the reduction due to the SI is 43% in 2005 and 50% in 2006. This means that in 2005 particles settle in areas where the sediment is more appropriate than in 2006 and, as a consequence, the final effective settlement (50 ind/m^2) with respect to the total number of particles released represents around 10% in both the years.

4.1.2. Spatial distribution

The spatial distribution of settled individuals was calculated on a regular grid (boxes 100 m wide) at the end of November for every year (Fig. 3). The result reflects the most productive areas in the lagoon. In the year 2005 the comparison between the spatial distribution, calculated in fishing area 2, and the measured distribution of spat larvae in the nursery area, reported by Boscolo Brusá et al. (2013) (at page 6, Fig. 4), shows a good agreement in the spatial presence/absence of spat larvae and in class of abundance. For the year 2006 the distribution is still consistent with the field data, even if the pattern is slightly different. The difference of settled larvae in year 2006 and year 2005 (see Table 3) indicates a relevant inter-annual variability. Moving from a typical year to a warmer one, the distribution moves from the borders close to the land toward the central part of the lagoon.

The distribution of settlement in WSF areas (Wild Seed Fishing, Fig. 4), indicates the suitability as a potential source of wild seed. The area 2 appears as the most profitable area with an average of 150 ind/m^2 and a maximum equal to 300 ind/m^2, followed by areas 7 (S.Leonardo) and 8 (Chioggia). In 2006 (not shown) the settlement in area 2 remains profitable (168 ind/m^2) and the area 4 has a considerable increase (from 35 to 112 ind/m^2) in agreement with the relevant inter-annual variability of settlement.

4.1.3. Timing in settlement

The temporal dynamic of the settlement (timing), including the mortality due to sediment composition, has been calculated month by month for both years as showed in Fig. 5. In the reference simulation (blue color) the settlement starts in the second half of May 2005

Table 2
Settlement in the whole lagoon. Before and after taking into account the sediment idoneity (SI) [ind/m^2].

Settlement	Reference		2050	2100
	2005	2006	2005	2005
Before SI	88	99	127	92
After SI	50	50	74	57
% reduction	43	50	42	38

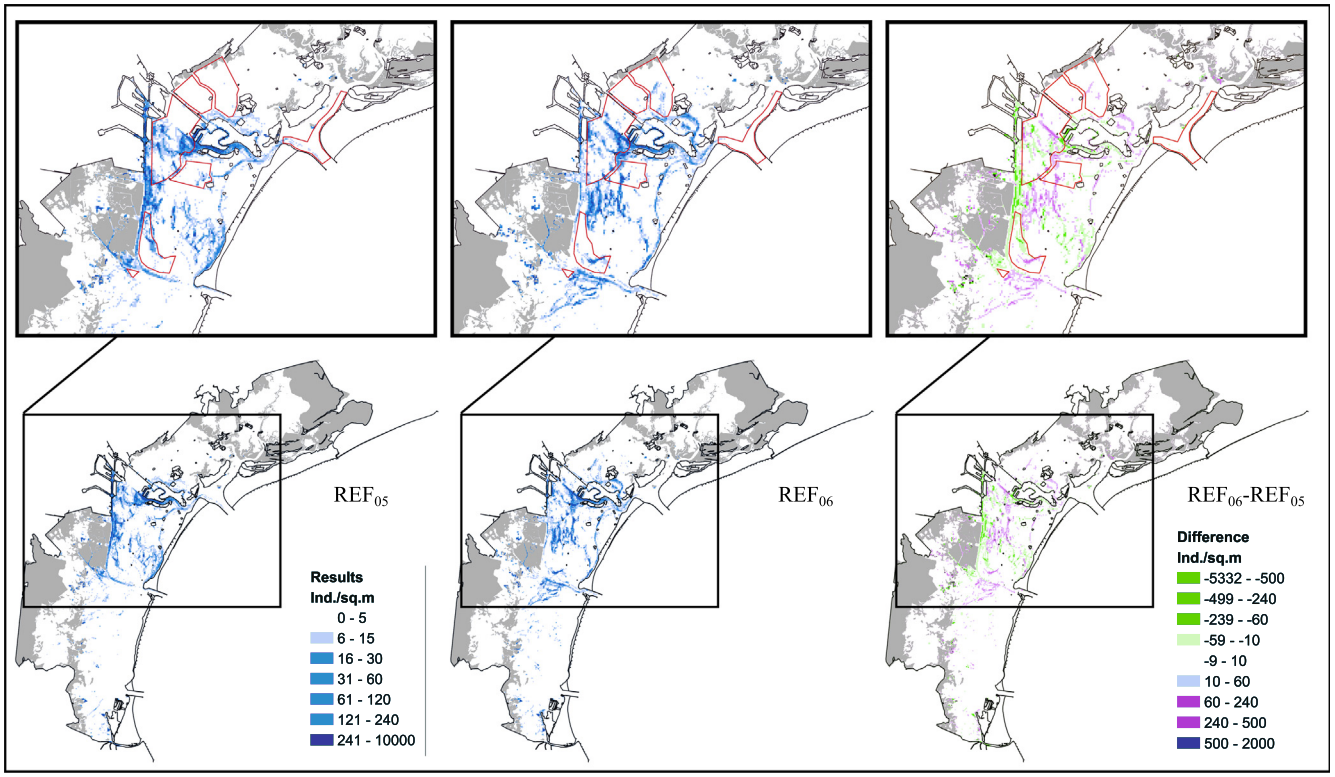

Fig. 3. Spatial distribution of effective settled organisms at the end of November 2005 (left panel), 2006 (central panel) and inter-annual variation 2006–2005 (right panel). Reference simulation, Unit: ind/m^2.

(less than 5 ind/m^2, 3% of the yearly settlement), increases in early July reaching two massive events in the second half of August (relevance 31% and 65% respectively). In year 2006 two more peaks are present: one in the second half of June and one in early November for a total of 4 settlement events. The peaks in 2006 are more numerous but less intense: the most relevant are the peaks in August (31%) and November (24%) followed by two peaks in June (13% and 8%).

The settlement timing in 2005 is in agreement with the literature about the Venice lagoon: the winter from December to February–March is a quiescent period, because of the reduced individual

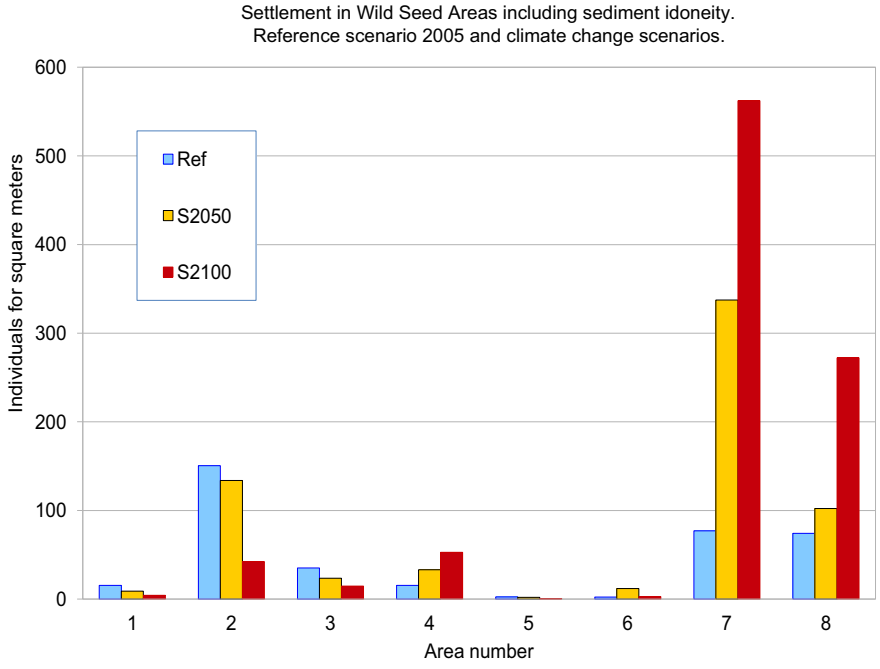

Fig. 4. Effective settlement of individuals in the Wild Seed Fishing areas in reference year 2005 and scenarios Unit: ind/m^2.

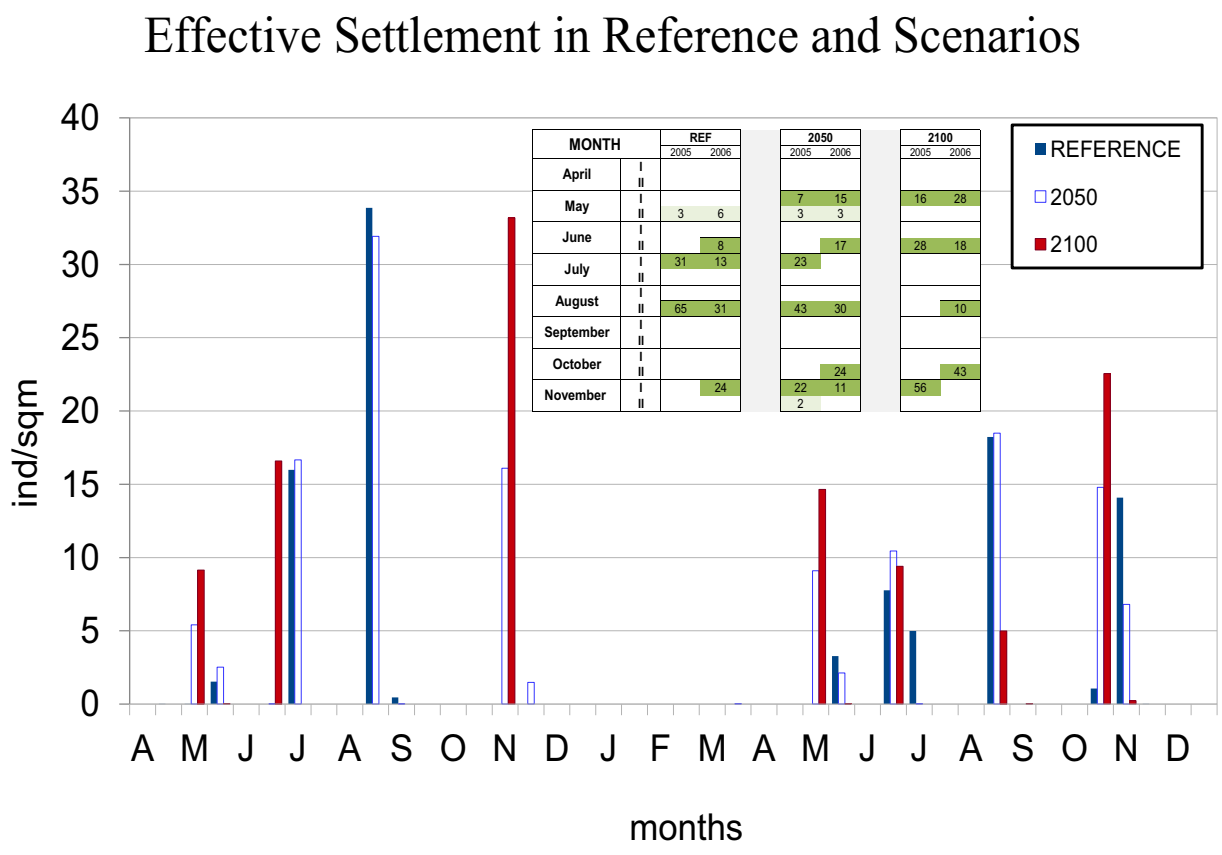

Fig. 5. Timing of effective settlement of individuals in the whole lagoon in 2005 and 2006 years. Reference simulation (blue), 2050 scenario (empty blue) and 2100 scenario (red). Unit: ind/m^2.

growth due to the low temperature, while the settling period extends from May to October–November having a discrete, massive and delayed behavior, reflecting the time necessary for individuals to reach the threshold length (Paesanti and Pellizzato, 2000). From the table included in Fig. 5, we can also notice that the effect of the warm year (2006) with respect to that of the typical year (2005) is to anticipate relevant settling events and to decrease the intensity of the settlement event in August, splitting it in different events.

4.1.4. Demographic history

The fate of each generation, corresponding to particles release events (5 generation in 2005, 6 in 2006, see Section 3.2.2), was analyzed to identify which of them is the most favorable for in settling and to evaluate the relevance of the different death causes. Table 3 reports the percentage of total alive and dead particles at the end of November 2006 (last column), specifying the relative percentage contribution of each particle generation. It also provides the possible reason of death (out of domain, temperature, age).

The generations of December and February do not lead to settlement and this lead us to consider late November as the end of the settlement season. The percentage of dead particles at the end of the two year simulation (November 2006) is 86%, the generations mostly contributing to this result are released in October, December, February and April. The main cause of mortality is the exit from the basin (68%) followed by temperature and age (10% and 7%, respectively).

Each generation contributes with an almost fixed percentage (10–12 %) to the mortality due to the exiting the domain. Only the generations of June and August of both years are less subjected to this risk (6–9 %), because they quickly settle on the bottom, growing faster with the summer water temperature.

Temperature mortality acts on the June generation of both years: in this month the balance between environmental temperature and time to reach the threshold length exposes the larvae to possible events of temperature higher than the lethal threshold. In year 2006, mortality from temperature also affects the August generation.

4.2. Climate change scenarios

4.2.1. Environmental variations

The total volume of the lagoon increases in the two years of simulation with relative percent of variation equal, on average, to 17% in 2050 and 35% in 2100 due to the water level rise. Despite this no significant changes in the currents average pattern was found.

The average water temperature in the simulated period increases from 17 °C in the REF to 19 °C in 2050 and to 21.5 °C in 2100, approaching the optimal temperature for the Manila growth (25 °C for growth and 20.5 °C for respiration).

The growth of larvae depends on both the change in average water temperature values and the variation in extreme values. For this reason we estimated the extreme upper (absolute maximum) and lower limits (absolute minimum) along the two years of simulation for the whole basin.

In the reference simulation, the maximum of average temperature and the absolute maximum temperature are 30.2 °C and 31.3 °C respectively, in the scenarios of climate change these value reach 32.3 °C and 33.5 °C in 2050 and to 34 °C and 35.3 °C in 2100. The maximum lethal temperature (32 °C for the growth and 35 °C for respiration) is a localized phenomena, therefore the mortality due to temperature remains coherent with the actual state.

The absolute minimum temperature and the minimum of average temperature in the reference are 1 °C and 4.1 °C respectively,

Table 3
Fate of each generation in reference and climate change scenarios until November 2006. *NLIVE* and *NDEAD* are the total percent of living and death particles; *nsed* is the percent of settled particles without sediment effect; *nout*, *ntem* and *nage* are the percent of particles death due to exit of domain, temperature or age respectively.

Sim	Birth	APR	GIU	AGO	OTT	DIC	FEB	APR	GIU	AGO	OTT	ALL
REF	nsed	1.74	14.78	30.60	0.	0.00	0.00	3.28	11.98	20.45	17.16	14.34
	nout	12.22	8.06	6.70	10.65	11.89	13.30	12.07	9.	6.99	9.24	68.22
	ntem	6.82	23.40	10.20	0.37	0.00	0.00	4.92	21.00	22.56	10.72	10.18
	nage	9.95	0.00	0.00	38.17	26.07	12.81	10.99	0.00	0.00	2.02	7.25
	NLIVE	1.74	14.78	30.60	0.	0.	0.	3.28	11.98	20.45	17.16	14.34
	NDEAD	11.38	9.20	6.55	11.67	11.67	11.67	11.12	9.67	8.25	8.80	85.66
2050	nsed	6.27	11.64	22.50	12.74	0.00	0.02	7.98	7.05	15.04	16.75	18.21
	nout	12.05	7.23	6.96	11.16	11.69	13.62	11.48	10.08	7.29	8.44	68.71
	ntem	5.51	27.78	10.72	0.13	0.00	0.00	6.30	17.08	21.47	11.00	10.48
	nage	0.00	0.00	0.00	0.00	75.60	24.40	0.00	0.00	0.00	0.00	2.60
	NLIVE	6.27	11.64	22.50	12.74	0.00	0.02	7.98	7.05	15.04	16.75	18.21
	NDEAD	10.83	9.63	7.22	9.39	12.23	12.22	10.45	10.66	8.88	8.50	81.79
2100	nsed	8.63	14.26	0.00	26.35	0.00	0.00	12.60	8.71	4.93	24.52	14.23
	nout	13.53	9.02	0.00	10.32	13.17	15.48	13.13	11.87	3.81	9.67	60.51
	ntem	2.58	11.12	44.25	0.03	0.00	0.00	1.17	6.98	30.93	2.93	22.60
	nage	0.	0.	0.	0.	76.26	23.74	0.00	0.00	0.00	0.00	2.66
	NLIVE	8.63	14.26	0.	26.35	0.00	0.00	12.60	8.71	4.93	24.52	14.23
	NDEAD	10.23	9.29	11.66	7.29	11.66	11.66	9.57	10.21	10.84	7.59	85.77

reaching 3 °C and 6 °C in 2050 and to 4.3 °C and 7.4 °C in 2100: the minimum temperature increases with climate change, but not to values sufficiently high enough in order to accelerate the winter growth of the organisms.

The average and maximum water temperatures of the basin in the REF_{05} are lower than in REF_{06}, confirming the second year as a "warm year" and the first year as a " typical" year. The comparison between the temperature ranges in REF_{06} and the range in the 2050 scenario for year 2005 ($S2050_{05}$) provides evidence that an actual hot year is comparable with a normal year in 2050. This means that the actual inter-annual variability is similar, in terms of water temperature, to the variability induced by the climate change in 2050. Comparison of water temperatures in REF_{06} and in $S2100_{05}$ shows that the maximum of temperature in 2006 is lower than the average and maximum temperature in scenario $S2100_{05}$: in this case the variation due to climate change in 2100 is greater than the actual inter-annual variability.

In the next section we will show the comparison between the reference simulations REF_{05} and REF_{06} to analyze the inter-annual variability in terms of settlements variations and the comparison between REF_{05} and the corresponding scenarios $S2050_{05}$ and $S2100_{05}$ to evaluate the effect of climate change.

4.2.2. Settlements variations

The settlement analysis in climate change scenarios ($S2050_{05}$ and $S2100_{05}$, Table 2) underlines the relevance of temperature range for growth, and also the crucial role of the combination of distribution pattern and sediment idoneity on the final settlement value. In $S2050_{05}$ the number of particles reaching the settlement is maximum (127 ind/m^2), also after the sediment idoneity reduction (74 ind/m^2, sediment mortality 42%). In $S2100_{05}$ the settlement is similar to REF_{05} and to REF_{06} (92 ind/m^2, 88 ind/m^2 and 99 ind/m^2 respectively), and the sediment mortality is the lowest (38%). This allows it to reach a final settlement in $S2100_{05}$ higher than in REF (57 vs 50 ind/m^2) and lower than the $S2050$ scenario (57 ind/m^2 vs 74 ind/m^2). The total effective settlement is 14% of the total number of released particles in 2050 and around 11% in 2100.

The spatial distribution of particles in the scenarios confirms the shift of patterns toward the central part of the lagoon. The effective settlement spatial distribution in $S2050_{05}$ and $S2100_{05}$ are shown in Fig. 6 (panel A 2050, panel B 2100) together with their respective difference with respect the REF_{05}. The shift of settlement pattern toward the central area and southward along the Malamocco-Marghera channel starts in the $S2050$ scenario and it becomes much more evident in the $S2100$ scenario. This shift agrees partially with the trend verified as inter-annual variability between reference years.

With respect to the actual WFS areas, Fig. 4 makes evident, for both scenarios, how the best settling place moves from area 2, which is recognized as the actual nursery area for the lagoon, to areas 7 and 8 located in the central basin corresponding to Malamocco-Marghera Channel and S.Leonardo area. Only the actual fishing area 4 shows a sign of slightly increasing settlement.

The settling timing in scenarios splits the most massive events or changes drastically the temporal period of settling, as shown in Fig. 5. Considering $S2050_{05}$ with respect to the REF_{05}, the most relevant settling events remain July (23%) and August (43%), also if their intensity is reduced. New events occur in November (22%) and early May (7%, see table in Fig. 4). Looking at $S2050_{06}$ scenario, the August settlement event remains, but with lower values than in REF_{06} (30%), the July event is anticipated to June (17%) and the early May event becomes stronger (15%). The autumnal settlement event is split between October and November. In $S2050_{05}$ there are 4 relevant settling events, and in $S2050_{06}$ they are 5. As noticed in inter-annual variability the effect of warmer conditions is to anticipate the settlement, splitting massive events into smaller ones. In the 2100 scenario the more intense change in climate conditions modifies drastically the timing of settling. The event in August almost disappears, anticipating to May and July; the most massive event is in November of $S2100_{05}$ (56%), while in $S2100_{06}$, it is anticipated to October (43%). In the first year in $S2100_{05}$ scenario are 3 relevant settling events and in the warmer $S2100_{06}$ scenario they are 4.

Finally we analyzed the fate of each generation for the whole period (2005 and 2006) for climate change scenarios (Table 3). The results indicate that initially the climate change will be favorable to settlement, but later it will start to decrease, changing the relevance of the different mortality causes. In the $S2050$ the percentage of successfully settled particles increases from 14 to 18%, while the percentage of dead particles decreases from the 86% to 82%. In the $S2100$ again the percentages become 14% and 86% respectively, as in the reference simulation. The main reason of mortality in $S2050$ remains the exit from the domain (around 68%) and the temperature (around 10%) followed by the age. The age represents the 7% of death causes for *REF* decreasing in $S2050$ to 2.5%. In $S2100$ the mortality due to the exit from the domain decreases (60%) and the mortality for temperature increases to 22%, while the mortality due to the age remains equal to $S2050$ (2.5%). This indicates that the temperature, in climate change conditions, becomes a more frequent mortality reason even if high temperature accelerates the larval development,

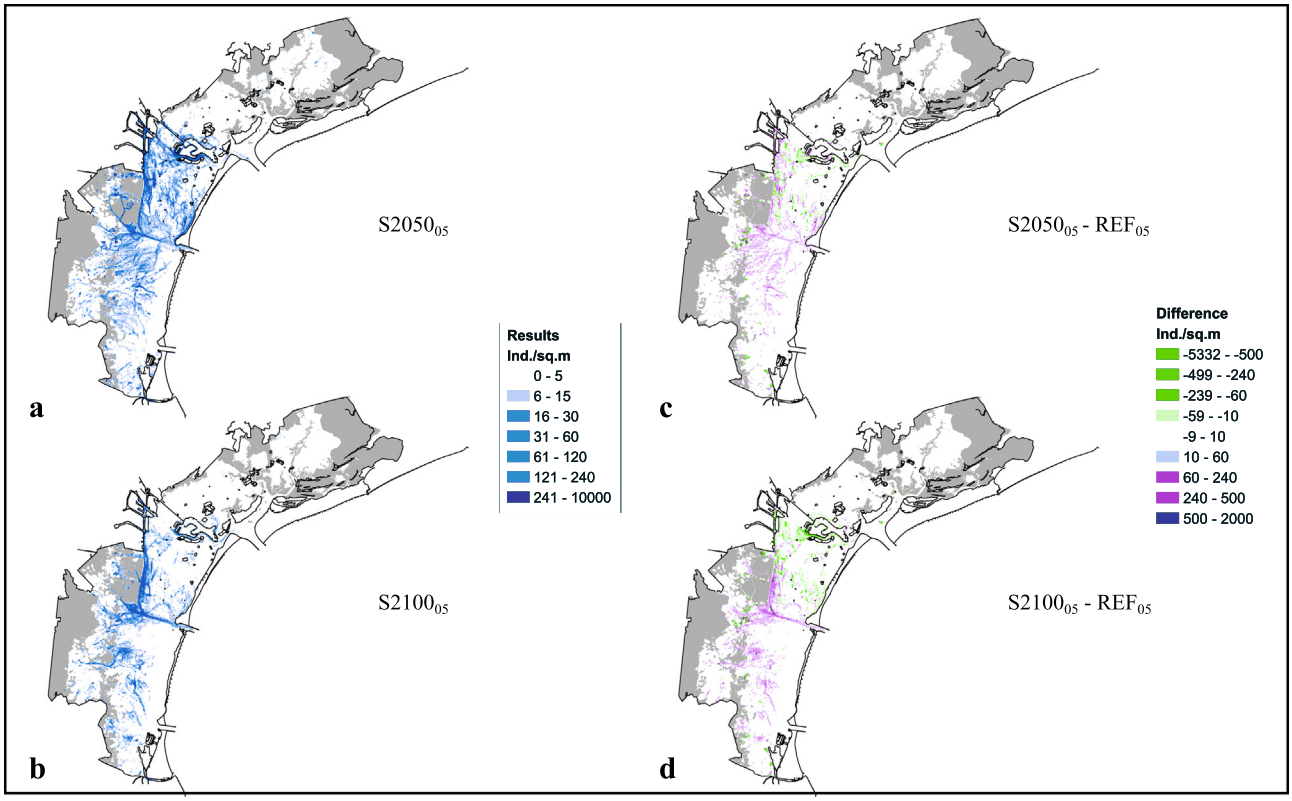

Fig. 6. Spatial distribution of settled organisms at the end of November in $S2050_{05}$ (top panel, left) and $S2100_{05}$ (bottom panel, left) and difference In respect of reference REF_{05} (top and bottom panels, right). Unit: ind/m^2.

allowing an earlier settlement and decreasing the probability to exit the lagoon.

5. Discussion

The model properly simulates the pattern of settlement of clam larvae, correctly identifying the areas where the natural settling process is more relevant. This indicates that the assumptions made on the emission frequency and place, on larval growth/settlement function and on the sediment survival function are acceptable as a first approximation.

The spatial distribution calculated in reference year 2005 is similar to the description given in Casale et al. (2001) for year 1999, who found that most of clams are in the central basin of the lagoon, identifying the area between Venice and the Industrial area as a nursery area with a high density of juvenile stage (up to 4000/ m^2). This area was confirmed in 2002 by Pessa and Mion (2005) and by Pellizzato et al. (2011) as nursery area for the whole period 2002–2007. In this study, the authors underline the large fluctuations observed in the density of individuals, confirming the role of this area as the most important nursery in the lagoon. Finally the comparison with the spat distribution reported in Boscolo Brusá et al. (2013) confirms the model performance in catching the distribution and settling processes. In addition another area of high abundance is identified by the model at the confluence of the Malamocco channel with the one passing along the industrial area (Fusina), in agreement with the estimation done by Vincenzi et al. (2011).

For what concerns the spawning time in the Venice lagoon, the literature reports a period from May to September or October. On the basis of data on post-settling cohorts, the settling timing starts in the period from late spring (April) to May and June and peaks of seed density can be found in September as a result of successive recruitment events, whereas the post-larvae arrive at highest density between June and August (Pellizzato et al., 2011). Despite the model spawning with constant frequency, it individuates correctly the temporal period of successful settlement (from April to September) and the successful spawned generations. It reproduces the correct time of most relevant settlement events (June and August), specifying the contribution of each released generation. In addition the model gives the estimation of mortality rates specifying the components related to dispersion, temperature and age, consistently with literature (Paesanti and Pellizzato, 2000).

In the literature the recruitment depends on multiple factors not all considered here (Olafsson et al., 1994), but focusing on the spatial settlement distribution and early recruitment, it appears strongly connected with the hydrodynamic and morphological conditions (Nambu et al., 2012; Pellizzato et al., 2011), and with the sand percentage in the sediment composition (Vincenzi et al., 2011; Pellizzato et al., 2011). The model results indicate that, as a first approximation, the current arrangement of spat groups is the result of the interaction of processes depending on hydrodynamic, sediment grainsize and temperature. These three factors are the main drivers for settlement in the Venice Lagoon for the simulated years, so other factors cited as nutrients are less relevant at least for that period.

In the literature the increase in water temperature is underlined to be a relevant factor in settlement: analyzing several years, the maximum values of juveniles was found by Pellizzato et al. (2011) in the year 2003, characterized to be a dry and hot year with severe hot waves events, and in the same year, the author found very different values of post-larvae with respect to the previous years (Pellizzato and Da Ros, 2005). The results of this study, on the simulated interannual variability between 2005 and 2006, underline the relevance of the direct effect of temperature on larval stage survival, but also

the crucial combination with hydrodynamic and sediment composition. The "typical" year (REF_{05}) has more conspicuous settlement events than a warmer year (REF_{2006}), which has a more events. At the end of the season more particles in the warm year are settled because of the event of late autumn, but the final percentages are almost comparable between the two years. The number of particles settled at the bottom in the warm year was later reduced by less suitable locations in terms of sediment (see Table 1). The larvae reach the threshold length faster under higher water temperatures, but settle in different positions and, due to the high heterogeneity of sediment idoneity, and this can reduce drastically the final number of successful settled particles.

The climate change has a direct effect on early life stages because of their sensitivity on temperature (Tezuka et al., 2012). In our study the climate change is related to the combined seasonal change in water temperature and salinity, water level, rain, and air temperature. It implies a local variation in the circulation and a global change of the water temperature in the basin. Looking at the scenarios the temporal variation of the settlement is connected to the temperature, while the spatial variation is more linked to the interaction between growth, dependent on temperature, and the different circulation patterns. The settlement events tend to be split in numerous smaller events in the case of relatively low increase of water temperature, whereas in the case of stronger variation the system rearranges the settling time moving massive settling events to early spring or late autumn.

The first change is consistent with the gradual and continuous variation of the water temperature toward the heating of the basin. The low incidence of temperature mortality is linked to the more fast maturation in water temperature conditions more similar to the optimal: the organisms can reach more quickly the threshold of settlement and so escape to the assumed causes of mortality. When temperatures exceed the maximum limit only a limited number of particles is also exposed.

Strong increase of water temperature reduces the settlement due to the temperature mortality: the particles are killed before they reach the threshold length reducing the final number of particles reaching the sediment.

The settlement variation with climate change indicates a shift of the pattern toward the central area of the lagoon and southward along the Malamocco-Marghera channel, partially in agreement with the patterns verified in a warm reference year (REF_{06}). The combination of temperature and circulation modifies the natural settlement and new areas (7 and 8) could be in the future favorite for the Venice lagoon.

The flexibility of the tool can be considered in terms of sensitivity and limits in its applicability in other lagoons or for other organisms. Our sensitivity studies demonstrated that the main factors influencing the result are: 1) the initial locations of seeding area in the model; 2) the estimation of temperature-dependent parameters; 3) the sediment idoneity function on the basis of grain-size composition. In order to apply the model to other systems and organisms, the first point is the most difficult to be solved and implies a good knowledge of the historical population of adult spawner. The second point can be approached by convergence algorithm, like in this study, to better estimate the parameter combination on the basis of field or laboratory available data on larval growth. Data on sediment grain-size composition within the system should be available and the functional form of sediment idoneity should be tested on the basis of the chosen organism. The resolution of sediment grain-size data influences the spatial reliability of the result and implies that a very detailed small scale study can be done only having a detailed sediment idoneity function. Finally the food availability appears not to be limiting at larval stage and the adopted equation in the individual based model is general enough to be applied to other similar organism (Bidegain et al., 2013).

6. Conclusions

As mentioned in Section 1 the open questions in aquaculture are the availability of spat to produce wild seed in terms of quantity and localization of nursery areas. This study demonstrated that our numerical tool can reproduces the well know distribution of schools of new-settled larvae in the Venice lagoon and allows us to identify and quantify the areas more subjected to natural settlement, coincident with the more relevant actual nursery area. This has some actual consequences for planning and management of the shell farms in the lagoon and can be used: 1) to protect the main nursery area by planning which human activities can be permitted in the surroundings; 2) to select which areas have enough natural enrichment of spat larvae to be designated as productive for shell farms: 3) to quantify the natural value of each area in terms of natural settlement and to translate it into an economic value for productivity.

Under climate change conditions the model application estimates that most parts of the natural settlement will be in different areas with respect to the actual nursery areas. This is a useful information for the local management authority that is going to establish a protected area in the WSF area 2 (Boscolo Brusá et al., 2013). Our results indicate the central part of the lagoon as the most suitable area for settlement in the future and, taking the results with reasonable confidence, the model could help the management authorities to design new suitable nursery areas. In general, the advice of the model is that the nursery protection cannot be seen as static in space and time, but will adapt to the different climatic condition to preserve the natural potential of the lagoon, which is a crucial aspect for the planning of a sustainable shell farming.

The results also indicate that initial climate warming can be beneficial for clam larvae settling, but stronger warming conditions could start reducing the spat availability. In both cases our study shows a trend in the settling timing to move toward early spring or late autumn, in order to survive the increasing water temperature during the summer. This behavior will influence the time of fishing activities and the relations of this benthic component with the other ecological components of the ecosystem. This is a general result of an adaptation life cycle of the organism similar to Manila clam, confirming the general adaptation reaction of biological temperate cycles to water temperature warming.

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